Differences in water relations and carbon assimilation in an invasive forb, *Centaurea maculosa*, compared with established flora in semiarid steppe

Judson P. Hill[1], Matthew J. Germino[1,4], Jon M. Wraith[2], Bret E. Olson[3] & Megan B. Swan[2]

[1]*Department of Biological Sciences, Idaho State University, Pocatello, ID 83209-8007, U.S.A.*
[2]*Department of Land Resources and Environmental Sciences, Montana State University-Bozeman, Bozeman, MT 59717-3120, U.S.A.*
[3]*Department of Animal and Range Sciences, Montana State University-Bozeman, Bozeman, MT 59717-2900, U.S.A.*
[4]*Corresponding author*

Corresponding author:
Matthew J. Germino
Department of Biological Sciences
P.O. Box 8007
Idaho State University
Pocatello, ID 83209-8007, USA
Tel.: (208) 282-3285
Email: germmatt@isu.edu

Running title: Ecophysiology of C. maculosa and established flora

Summary

1. Whether differences in carbon and water relations between exotic and native plants contribute to invasions of semiarid steppe of western North America is unknown. Plant-soil water relations and carbon assimilation (A_{net}) were measured for European spotted knapweed (*Centaurea maculosa*), and dominant rangeland species of southwestern Montana, USA: *Pseudoregneria spicata*, *Pascopyron smithii, Bromus inermis*, and *Rudbeckia hirta*.

2. No differences in A_{net} and water use efficiency (WUE; mol CO_2/H_2O) occurred between the species under three water treatments in a greenhouse, where roots were confined from foraging by pots. However, in the field, *Centaurea* had greater A_{net} and a longer growth season than the other species for 2 years of variable climate. Moreover, *Centaurea* had smaller declines in A_{net} than the other species during seasonally dry periods.

3. In the field, WUE of *Centaurea* was more responsive to large decreases in soil water than WUE of the other species. Also, *Centaurea* consistently maintained greater xylem water potentials from predawn to midday, despite having 2-fold greater evapotranspiration compared to the other species.

4. These ecophysiological differences may reflect greater soil water extraction in *Centaurea*, which, combined with higher WUE under severe water limitations, contributes to superior A_{net} compared to established flora.

Key-words: exotic plants, grasslands, photosynthetic gas exchange, water status

Introduction

Rapid increases in the distribution and abundances of invasive plants have been postulated as the greatest deterrent to ecosystem function in the vast semiarid steppe of western North America. Replacement of native shrub and bunchgrass communities by exotic annual grasses (eg. *Bromus tectorum*) and perennial forbs (eg. thistles, *Centaurea*, and *Euphorbia* sp.) has occurred in many areas of this region. The persistence of *B. tectorum* and similar grasses has been attributed to differences in water and nutrient relationships between the invasive and native species, which, along with altered fire frequencies, can lead to modification of environmental resources in favor of the invasive species (eg. Booth, Caldwell & Stark 2003). However, whether invasive perennial forbs differ from native plants of semiarid steppe in their use of limiting soil resources is not well known.

One of the most problematic invasive species in this region is European spotted knapweed (*Centaurea maculosa* Lam.; DiTomaso 2000). Much of the research on *C. maculosa* has focused primarily on its control and suppression (eg. Tyser et al. 1998; Griffith & Lacey 1991), and a fundamental understanding of mechanisms contributing to the success of *C. maculosa* and similar invasive forbs is lacking. Allelopathy may contribute to *C. maculosa's* success (Bais et al. 2003; Ridenour & Callaway 2001), whereas other studies suggest that knapweed is a more consummate user of nitrogen and phosphorous and could have an advantage under conditions of nutrient enrichment (Olson & Blicker 2003; Zabinski, Quinn & Callaway 2002; Blicker, Olson & Engel 2002; Herron et al. 2001). However, whether interspecific differences in water relations and corresponding photosynthesis could contribute to the invasiveness of *C. maculosa* in rangelands is not known, despite the role of water limitations in semiarid plant communities (West 1983).

Photosynthetic carbon assimilation (A_{net}) is a primary determinant of plant growth (Lambers & Poorter 1992), and is a useful measure of plant performance, especially with consideration of leaf area and arrangement in whole plants (Pearcy et al. 1987; Bazzaz, Chiariello & Coley 1987). Carbon assimilation could influence the number of seeds produced by an individual by increasing maternal plant mass and resources for allocation (Gurevitch, Scheiner & Fox 2002). Invasive species are often characterized by rapid growth rates compared with native plants (Williams & Black 1993; Wedin & Tilman 1993). Carbon assimilation rates are also often greater in invasive than native species, as demonstrated in tropical rainforests and mesic grasslands (Durand & Goldstein 2001; Smith & Knapp 2001; Baruch & Goldstein 1999; Pattison, Goldstein & Ares 1998; Williams, Mack & Black 1995), though photosynthetic properties other than assimilation rate *per se* appeared most relevant to the success of an invader of wetlands (Nagel & Griffin 2004). Less is known about the potential importance of interspecific differences in A_{net} in semiarid communities, which, in turn, are likely to arise from interspecific differences in water relations. Water relations may vary among species as a result of differences in soil water acquisition, which is often a function of rooting depth and distribution (Craine et al. 2003; Donovan & Ehleringer 1994; Cody 1986; Davis & Mooney 1986), or differences in evaporative losses and photosynthetic water use efficiency (WUE; μmol CO_2/mmol H_2O). Differences in A_{net} and water relations between invasive and established species might provide insight into drought stress avoidance or conservation strategies that benefit invasive species when soil water is limiting.

Our objectives were to determine: 1) if *C. maculosa* had greater carbon assimilation than several semi-arid, rangeland species which dominate sites that are frequently invaded by *C. maculosa*, and 2) whether greater A_{net} in *C. maculosa* was correlated with plant water status.

Moreover, we determined whether interspecific differences in carbon assimilation and water relations reflected different strategies for tolerating or avoiding seasonal drought stress. Invasive plants may have greater flexibility or plasticity in ecophysiological characteristics than native plants of other habitats, which can contribute to invasiveness (Williams et al. 1995). We therefore also determined whether *C. maculosa* was more flexible in its carbon assimilation and water relations among sites and time, compared with established species.

Land management practices can strongly affect species composition and corresponding soil water patterns in semiarid rangelands (Germino and Seefeldt *unpublished*). Moreover, precipitation is relatively more variable in semiarid than in more mesic habitats (Frank & Inouye 1994). Thus, an understanding how water availability affects the performance of invasive compared with native plants could yield important insight on temporal variations in invasions. Interspecific differences in water relations and photosynthesis in exotic compared with native species could therefore yield crucial, mechanistic insight on plant invasions of grasslands.

Methods

This study consisted of a greenhouse experiment in the summer of 2001, and field observations in the summers of 2002 and 2003 on *C. maculosa* and the dominant rangeland grasses *Pascopyron smithii* Rydb (western wheatgrass), *Pseudoregneria spicata* Pursh A. Love ssp. *spicata* (bluebunch wheatgrass), *Bromus inermis* Leyss. (smooth brome), and *Rudbeckia hirta* L. (black-eyed susan). The greenhouse study determined whether *C. maculosa* differed from grass competitors in carbon assimilation or water use efficiency across three tightly controlled soil water regimes. In the field, plant gas exchange and xylem pressure potential were measured to determine how *C. maculosa* compared with coexisting natural flora where roots

were not bound by pots. Plants were examined at a site near Leverich Canyon 10 km south of

Bozeman, which was relatively wetter than the second site, approximately 16 km east of Helena,

Montana. Soils at Leverich were a silty loam overlaying gravelly and sandy loams below about

25 cm. Soils at Helena were a silty clay loam overlaying clay below about 25 cm.

GREENHOUSE

Centaurea maculosa, *P. spicata*, and *A. smithii* were grown from seed in a greenhouse

with constant light and temperature under three different soil water matric potentials of -1 MPa,

-0.1 MPa, and -0.01 MPa (hereafter referred to as the dry, mesic, and wet levels, respectively)

during the summer of 2001. Seeds of each species were planted in 18 columns, each 0.1 m in

diameter and 0.4 m tall, with six columns assigned to each of the three water treatments, for a

total of 54 columns. These columns were randomly assigned to one of six blocks. Seeds

germinated and grew 4 months under the three water levels. Water treatments were maintained

by adding enough water to establish target soil matric potentials three times each week. Soil

matric potentials were determined by first measuring gravimetric water contents of the columns,

and then calculating soil water content from measured soil water retention curves (Or & Wraith

1999). Following 4 months of growth during the summer under natural light, photosynthetic gas

exchange was measured for four consecutive days on three randomly chosen individuals of each

species under each soil water treatment. Carbon assimilation (A_{net}), stomatal conductance to

water vapor (g^{st}), and transpiration rate (E) were determined with a portable, closed-flow gas

exchange system equipped with a CO_2 controller and an artificial red-blue light source (LI-6400,

LI-COR Inc., NE, USA). Water use efficiency (WUE) was calculated as *A/E* (μmol CO_2/mmol

H_2O). Gas exchange parameters were calculated on a projected leaf area basis, at ambient light

levels for leaves oriented perpendicular to the sun. Projected leaf area was determined from digital pictures taken of sampled leaves in their natural orientation to the sun (zenith and azimuth). Leaf area was determined in each image to a resolution of 0.1 cm^2 using image processing software (Scion Co., MD, USA).

FIELD OBSERVATIONS

Gas exchange and plant water status of *C. maculosa*, *P. spicata*, and *B. inermis* were measured at the two sites in southwestern Montana during the summers of 2002 and 2003. Both sites had areas dominated by *C. maculosa* and by patches of the perennial grasses, *P. spicata* (Helena) or *B. inermis* (Leverich). At the Helena Site, *B. inermis* was also present but was not the dominant species, and was only measured there in 2003. Photosynthetic gas exchange and plant water status were measured at each site three times during the growing season to evaluate temporal limitations in carbon uptake during seasonal periods of high to low water availability. Leaf-level gas exchange was measured on five individuals of each species starting at 0800 on days with clear-sky conditions. Representative leaves of each species acclimated to full sunlight were measured. Gas exchange parameters were computed as described above, except *E*. Transpiration was estimated from the product of stomatal conductance and leaf-air vapor deficit (von Caemmerer & Farquhar 1981). Leaf-air vapor pressure deficit was determined from separate measurements of relative humidity and leaf and air temperatures using hand-held instruments taken prior to inserting leaf into measurement chamber (Hygro-Thermo-Anemometer, Extech, MA, USA; PM Plus infrared thermometer, Raytek, Inc., CA, USA).

Field microclimate conditions were recorded at both sites using dataloggers (CR10X, Campbell Scientific, Inc, UT, USA). Three spatial replicates of air and soil temperatures were

monitored every 30 and 60 minutes, respectively, at 5 cm and 1 m depth and height. During the 2003 season, time domain reflectometry (TDR; Model TDR 100, Campbell Scientific, UT, USA) was used to monitor volumetric soil water contents at the Leverich and Helena field sites from June through August. Volumetric soil water contents were also determined under four monospecific stands of *C. maculosa* at each site, at incremental depths of 20 cm down to 140 cm at Leverich and to 120 cm at Helena, three times during the season, using a neutron moisture meter (503DR, California Pacific Nuclear, CA, USA).

PLANT WATER POTENTIAL

Plant water status was determined by measuring xylem pressure potentials (Ψ) during the two field seasons. *Rudbeckia hirta* L. (black-eyed Susan) was measured in mid-July 2003 at the Leverich Site, in addition to *C. maculosa*, *P. spicata*, and *B. inermis*. *Rudbeckia hirta* was the least abundant of measured species, but was included to provide another forb of the same family (*Asteraceae*) to compare with *C. maculosa*. Five representative individuals of each species were selected randomly from within the community. Measurements were repeated two times each day at predawn and 1600 h using a Sholander type pressure chamber (Plant Moisture Stress Instruments Co., Oregon, USA). Representative terminal shoots, approximately 4–8 cm long, were collected from the mid-canopy of each species at each measurement period. Each sample was excised and immediately placed into the pressure chamber for measurement.

STATISTICS

Gas exchange measurements were analyzed with ANOVA using JMP software (SAS Institute, NC, USA). Data were square-root transformed when assumptions of normality were

not met. Greenhouse A_{net} and water use efficiency (WUE) were analyzed with soil water treatment and species as main factors. Field gas exchange was analyzed with multiple one-way ANOVA to determine the differences between the two years, the two sites, and the three species.

Results

GREENHOUSE

Mean carbon assimilation (A_{net}) rates for a four-day measurement period in the greenhouse increased as water level increased ($F_{2, 99} = 17.08$, $P < 0.0001$) similarly for all species ($F_{2, 99} = 1.96$, species by treatment interaction, $P = 0.147$; Figure 1). Water use efficiency (WUE) decreased with increasing water levels ($F_{2, 99} = 8.35$, $P = 0.0005$), similarly for all species ($F_{2, 99} = 0.21$, $P = 0.810$).

FIELD MICROCLIMATE

Mean growing season temperatures were 1-2° greater in 2003 than in 2002, and Helena was generally warmer than the Leverich Site both summers (Table 1). However, during approximately two weeks in July 2003, the Leverich Site had record high temperatures compared with long-term observations (NOAA), and had greater maximum temperatures compared to the Helena Site. Mean annual precipitation since about 1920 was 442 ± 22 mm/yr and 295 ± 14 mm/yr at weather stations closest to the Leverich and Helena Sites, respectively. During the May through September growing season, Helena received 263.4 mm and 120.4 mm precipitation in 2002 and 2003, respectively; and Bozeman received 362 mm and 161.5 mm in 2002 and 2003, respectively (Western Regional Climate Center, Desert Research Institute, Reno, NV).

Volumetric soil water contents (VWC) that correspond approximately with the lower limit of plant-available water (ie. soil water potential near –1.5 MPa) are about 25% and 15% for clay and loam soils, respectively (Nobel 1983). However, unmeasured variables such as bulk density, organic matter, and deviations of our soils from being either pure clay or loam likely affect the water-retention characteristics of soils we studied (Or & Wraith 1999). Inferences on water availability based on VWC measured at the sites (Fig. 2 and 3) must therefore be made with caution. We therefore highlight relative changes in VWC that were both large and also correspond with our measurements of significant changes in the ecophysiology of plants. In 2003, mean VWC in the top 30 cm of soil was greater (by 33%, initially) in the relatively loamy soils at Leverich compared with the more clay-rich soils of Helena, until the second week of July. During this unusually warm week of July, soil water contents at the Leverich Site decreased to VWC levels below those measured at Helena (Fig. 2). However, these near-surface VWC values became within the approximate range for availability to plants only at the Leverich Site, and only during June and July (estimated from Fig. 2). At Leverich in July 2003, VWCs under monospecific stands of *C. maculosa* were in the range of plant-available water at all of the measured depths (estimated from Fig. 3). In contrast, only VWC near 1 m depth were possibly in the approximate plant-available range at Helena in July 2003, and, subsequently, VWCs were most likely below plant-available levels (Fig. 3). By August 2003 at the Leverich Site, only soils deeper than 1.2 m had VWCs that could have been within the plant-available range (estimated from Figure 3).

FIELD PHOTOSYNTHESIS

Leaf-level carbon assimilation of all of the species was two-fold greater in 2002 than in the relatively drier summer of 2003 at the Helena ($F_{1, 51}$ = 32.98, P < 0.0001) and Leverich sites ($F_{1, 44}$ = 7.01, P = 0.012). Carbon assimilation was 48% greater at the Leverich than at the Helena Site in both years ($F_{1, 96}$ = 11.97, P = 0.0008). *Centaurea maculosa* had greater A_{net} than the co-occurring, dominant rangeland grasses at the Helena ($F_{2, 51}$ = 3.60, P = 0.035) and Leverich sites in both years ($F_{1, 44}$ = 19.0, P < 0.0001, Fig. 4). Additionally, positive values of A_{net} were measured later into the growth season for *C. maculosa* during the relatively wetter 2002 season. Rosettes of *C. maculosa* senesced earlier (by mid-August) in 2003 than in 2002 at both sites (Figure 4). Before our study, foliage remained green at the Leverich Site until early October in 2000 and 2001 (MJ Germino, *unpublished*). Although rosette leaves of *C. maculosa* had senesced, active photosynthetic tissue in the form of green stems and cauline leaves persisted later in the season.   Mean *E* over all sites and dates was more than 2-fold greater for *C. maculosa* (5.4 ± 1.3 mmol m^{-2} s^{-1}) than for all of the grasses combined (2.5 ± 0.4 mmol m^{-2} s^{-1}; T_8 = 2.15, P = 0.03)

Water use efficiency of *C. maculosa* was similar to the grasses during 2002. However, WUE of *C. maculosa* was greater than the grasses for all sampling dates at Helena, and during late summer at Leverich during 2003 (Fig. 4). Water use efficiency of *C. maculosa* was 102% greater than for *P. spicata* ($F_{1, 19}$ = 29.63, P <0.0001) and 32% greater than for *B. inermis* ($F_{1, 17}$ = 3.07, P =0.099) at the Helena Site during 2003. At the Leverich Site during July 2003, WUE of *C. maculosa* was 75% greater than for *B. inermis* ($F_{1, 9}$ = 5.97, P = 0.040; Fig. 4).

Water use efficiency also varied considerably more among sampling dates in *C. maculosa* than in the grasses. Water use efficiency in *C. maculosa* at the Helena site in 2002 was

252% greater in August than July ($F_{2, 13}$ = 38.80, P < 0.0001); whereas WUE in *C. maculosa* at

the Leverich Site increased 93% across the same months ($F_{2, 14}$ = 6.80, P = 0.011; Fig. 4). In

June and July of 2003 at Helena, WUE in *C. maculosa* was 82% greater than WUE of the same

population of *C. maculosa* the previous, relatively wetter year ($F_{1, 19}$ = 22.80, P = 0.0002). In

contrast to *C. maculosa*, variations in WUE of the grasses were much smaller, with maximum

decreases in WUE of 42% for *B. inermis* and 21% for *P. spicata* as soils dried in 2003 (Fig. 4).

PLANT WATER POTENTIAL

Although *C. maculosa* did not have the greatest predawn water potential, it maintained a

relatively higher Ψ during the day than the other species. Plant water potential in *C. maculosa*

decreased only 34 ± 9 % from predawn to midday compared with 51 ± 1%, 78 ± 4%, and 68%

decreases in *P. spicata*, *B. inermis,* and *R. hirta*, respectively (Figure 5). Accordingly, *C.

maculosa* had midday water potentials that were 183% and 110% greater than *P. spicata* and *B.

inermis*, respectively. For example, during June 2003, mean Ψ of *C. maculosa* at Helena

decreased from −0.94 ± 0.09 MPa in the morning to −1.12 ± 0.1 MPa in the afternoon, whereas

the Ψ of *P. spicata* decreased from −1.69 ± 0.9 MPa to −3.45 ± 0.12 MPa from morning to

afternoon, respectively. During the same time at the Leverich Site, Ψ of *C. maculosa* decreased

from −0.58 ± 0.02 to −0.92 ± 0.10 MPa from morning to afternoon, whereas the Ψ of *B. inermis*

decreased from −0.40 ± 0.03 to −1.55 ± 0.11 MPa, respectively. *Centaurea maculosa* was able

to maintain greater A_{net} and higher Ψ values than *B. inermis* and *P. spicata,* but did not appear to

have greater A_{net} than the other species when Ψ became lower than about −1.0 MPa, although

data points were scarce for *C. maculosa* below about −1.5 MPa because we rarely observed it

becoming so dry (Fig. 6).

Discussion

Previous studies demonstrated greater carbon assimilation (A_{net}) in invasive compared to native plants of habitats that were relatively mesic compared with our semiarid sites (Baruch & Goldstein 1999; Pattison et al. 1998; Smith & Knapp 2001). Traits that enhance light interception, a major limiting resource to plants in these studies, were correlated with greater A_{net}. Similarly, our results provide evidence for greater A_{net} in an invasive than a native species on semiarid rangelands (Fig. 4). Furthermore, greater A_{net} corresponded with higher xylem pressure potentials in *C. maculosa* than in established plants (Figs 4 & 5), indicating that greater A_{net} was related to traits that enhance water relations in our water-limited communities. Greater instantaneous A_{net} of *C. maculosa*, combined with several fold greater leaf area (Schwartz & Germino *unpublished*) and a longer season for carbon assimilation, likely lead to much greater annual carbon assimilation for *C. maculosa* than established flora. However, this assertion has not been formally tested with season-long measures of whole-plant carbon gain. Greater yearly carbon assimilation could contribute to greater growth and reproductive output in *C. maculosa* than the perennial grasses (Gurevitch et al. 2002).

Centaurea maculosa maintained higher (less negative) xylem pressure potentials (Ψ) than established species during daily solar periods (Fig. 5) despite greater evapotranspiration per unit leaf area, and especially per whole plant (based on relatively greater leaf area in *C. maculosa*). *Centaurea maculosa* must have acquired more water for it to maintain higher Ψ than established species, despite having higher evaporative water loss and no apparent advantages in water storage (i.e. no signs of succulence). Greater utilization of soil water in *C. maculosa* compared with native grasses agrees with previous findings of lower soil water contents under

experimental communities with *C. maculosa* than nearby areas with perennial grasses but no *C. maculosa* (Sperber 2001; Swan and Wraith *unpublished*). Rangelands dominated by *Centaurea solstitialis* also had lower soil water contents than nearby rangelands without *C. solstitialis* (Gerlach 2004). Greater uptake of soil water appears to benefit *C. maculosa* by leading to the maintenance of high Ψ even as evapotranspiration water losses occur during days. Greater Ψ in *C. maculosa* appears to lead to greater A_{net} compared with established species (Figs 4, 5, 6).

Most of the extra water extracted by *C. maculosa* compared with established species was probably derived from deeper (> 1 m deep) soils (Fig. 3). *Centaurea maculosa* depletes more soil water than grasses in deeper (eg. ca. < 0.6 m) soil horizons (Sperber 2001; Swan & Wraith *unpublished*). The lack of differences in A_{net} among the species under greenhouse conditions (Fig. 1), where roots of *C. maculosa* were unable to forage for water that other species could not access, is evidence that use of deeper water sources is a potentially a major contribution to the greater A_{net} in *C. maculosa* compared to established species in the field. Volumetric water content levels tend to be higher and less variable over time in soils near 1 m depth than closer to the surface in the sites we examined (Fig. 3, Sperber 2001). Most precipitation at our sites occurs from December through May, when evaporation and evapotranspiration rates are relatively low, allowing precipitation to infiltrate to soil horizons that are deeper than where most roots occur in grasslands (Weaver & Albertson 1943). Our data provide some support for the hypothesis that deep soil moisture provides a more stable and abundant source of water to *C. maculosa* than to grasses, which, in turn, may lead to greater water status and carbon assimilation in *C. maculosa*. Use of deep water would confer an advantage for *C. maculosa* on grasslands and disturbed (eg. burned) sagebrush lands that have fewer perennial forbs and shrubs, and correspondingly greater abundances of relatively deep soil water. This hypothesis would be

confirmed with measurements of soil water content at different depths under grasses and *C. maculosa.*

Plant species that persist under low soil water conditions often have adaptations for greater WUE than species from mesic environments (Anderson et al. 1997). *Centaurea maculosa* did not use water more efficiently than other species in the greenhouse, or in the field under relatively wetter conditions at both sites (Figs 1 & 4). Similarly, in a recent greenhouse and field study, *C. maculosa* did not use water more efficiently than *P. spicata* and *Festuca idahoensis* based on carbon isotope discrimination (Blicker, Olson & Wraith 2003). Carbon isotope discrimination provides a time-integrative measure of WUE that is unable to detect fine-scale fluctuations in WUE that may include potentially critical events, such as the unusually warm and dry days in the summer of 2003 (Fig. 4). Indeed, the few cases where WUE was greater in *C. maculosa* than established flora happened under the driest conditions of the study period (Fig. 4).

In unpredictable environments, a flexible WUE could allow plants to exploit favorable conditions while maintaining growth during drier conditions (Silim et al. 2001). *Centaurea maculosa's* greater flexibility of WUE probably contributed to it extending its growing season beyond that of grasses, whose primary strategy for avoiding drought is dormancy (Fig. 4). Flexibility in WUE may enable high A_{net} when water is abundant, while possibly conserving soil water as it becomes scarce and consequently increasing the duration of *C. maculosa's* seasonal carbon assimilation. Water conservation may not be advantageous to a species that forfeits soil water to competitors. However, *C. maculosa's* greater WUE corresponded in time with apparent reliance on deep moisture (Sperber 2001; Swan and Wraith *unpublished*) that is presumably not

available to the relatively shallow-rooted grasses. Moreover, grasses appeared to begin entering

dormancy as WUE increased in *C. maculosa* (Fig. 4).

CONCLUSIONS AND IMPLICATIONS

Our results indicate several ecophysiological mechanisms that may contribute to the

invasiveness of *C. maculosa* in semiarid rangelands. Greater A_{net} in *C. maculosa* than in the

established species appears to result from greater acquisition of soil water and adjustment of

stomatal conductance to enable persistence of A_{net} as soil water becomes scarce. Although these

mechanisms are not likely the sole reason for *C. maculosa's* success, they are potentially key

factors that enable *C. maculosa* to survive and proliferate in rangelands of the western North

America. Moreover, these mechanisms support the importance of a greater ability to extract a

limiting resource by invasive compared with established species as a factor enhancing invasions.

Centaurea maculosa's greater water relations and A_{net} compared to established vegetation

may apply to other invasive perennial forbs on semiarid rangelands. Sixty percent of the 46

exotic plants considered to be invasive problems on rangelands (Pyke 1999) are deep-rooted

perennials like *C. maculosa* whose phenology, rapid growth patterns, growth form, and other

traits seem to contrast growth strategies of native plants or rangelands (i.e. shrubs, bunchgrasses,

perennial forbs). Whereas relatively undisturbed communities in sagebrush steppe use soil water

relatively completely (Anderson et al. 1987), most rangelands regularly experience disturbances

(eg. fire) that preferentially exclude deep-rooted species and lead to corresponding increases in

deep soil water (Germino and Seefeldt *unpublished*). We hypothesize that increases in deep soil

water may be a key way these disturbances encourage site dominance by *C. maculosa* or other

deep-rooted perennial forbs.

Acknowledgements

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Table 1. Average daily mean, maximum, and minimum air and soil temperatures ($\pm$ 1 SE) at the Leverich and Helena field sites during June, July, and August of 2002 and 2003 at 1 m air (n=2), 5 cm air (n=4), 5 cm soil depth (n=3), and 1 m soil depth (n=3).

Statistic	Location	Height/Depth	2002		2003	
			Leverich	Helena	Leverich	Helena
Mean	Air	1 m	17.7 ± 0.4	18.6 ± 0.4	18.6 ± 0.5	20.2 ± 0.5
		5 cm	18.1 ± 0.4	19.7 ± 0.4	19.4 ± 0.5	21.8 ± 0.5
	Soil	5 cm	18.4 ± 0.3	20.5 ± 0.3	20.5 ± 0.3	21.8 ± 0.4
		1 m	15.0 ± 0.3	14.8 ± 0.1	14.8 ± 0.3	14.6 ± 0.3
Maximum	Air	1 m	27.9 ± 0.6	29.4 ± 0.6	34.8 ± 0.7	30.7 ± 0.6
		5 cm	34.2 ± 0.6	37.4 ± 0.6	29.1 ± 0.7	42.0 ± 0.8
	Soil	5 cm	23.1 ± 0.4	26.9 ± 0.4	26.8 ± 0.5	28.4 ± 0.5
		1 m	17.3 ± 0.5	14.9 ± 0.1	16.3 ± 0.3	14.7 ± 0.3
Minimum	Air	1 m	7.5 ± 0.4	8.8 ± 0.4	8.4 ± 0.3	8.9 ± 0.4
		5 cm	5.3 ± 0.4	7.0 ± 0.4	7.8 ± 0.4	6.9 ± 0.4
	Soil	5 cm	15.0 ± 0.2	15.6 ± 0.3	15.5 ± 0.3	16.3 ± 0.4
		1 m	13.7 ± 0.3	14.7 ± 0.1	13.6 ± 0.2	14.5 ± 0.3

Figure Captions

Figure 1. Mean photosynthesis and water use efficiency (A/E) of *C. maculosa* (solid symbols), *A. smithii* (open, square symbols), and *P. spicata* (open, round symbols) in a greenhouse under three target soil water matric potentials: Dry (-1.0 MPa), Mesic (-0.1 MPa), and Wet (-0.01 MPa). (n=4 daily means; 3 individuals per day)

Figure 2. Monthly average of volumetric soil water content ($\pm$ 1 SE) for the top 30 cm of soil at Leverich (solid symbols) and Helena (open symbols) field sites as determined with TDR probes during the 2003 season (n=24). The estimated permanent wilting levels for plants are indicated by a dashed line for clay soils (25 %), and a solid line for loamy soils (15 %), according to Nobel (1983).

Figure 3. Volumetric soil water content at depths of 20 cm (solid symbols), 80 cm (open symbols), 120 cm (triangular symbols), and 140 cm (square symbols) under monospecific stands of *C. maculosa* at Leverich and Helena field sites during June, July, and August 2003. The estimated permanent wilting levels for plants are indicated by a dashed line for clay soils (25 %), and a solid line for loamy soils (15 %), according to Nobel (1983).

Figure 4. Daily maximum leaf-level photosynthesis ($\pm$ 1 SE) and corresponding WUE (*A*/E) of rosette leaves of *C. maculosa* (solid symbols), *P. spicata* (open, round symbols), and *B. inermis* (triangular symbols) in natural communities across 2002 and 2003 at two field sites in SW Montana. Each day leaf-level gas exchange was measured on n=5 plants per species.

Figure 5. Mean percent change in plant water potentials mesasured at predawn and midafternoon, at two field sites in SW Montana during the 2002 and 2003 growth seasons for *C. maculosa* (CEMA), *P. spicata* (PSSP), *B. inermis* (BRIN), and *R. hirta* (RUHI). (n = # days; 5 measurements per/day)

Figure 6. Relationship between photosynthesis and plant water potential of *C. maculosa* (CEMA), *P. spicata* (PSSP), and *B. inermis* (BRIN) at two field sites in SW Montana during the 2002-2003 growth seasons.
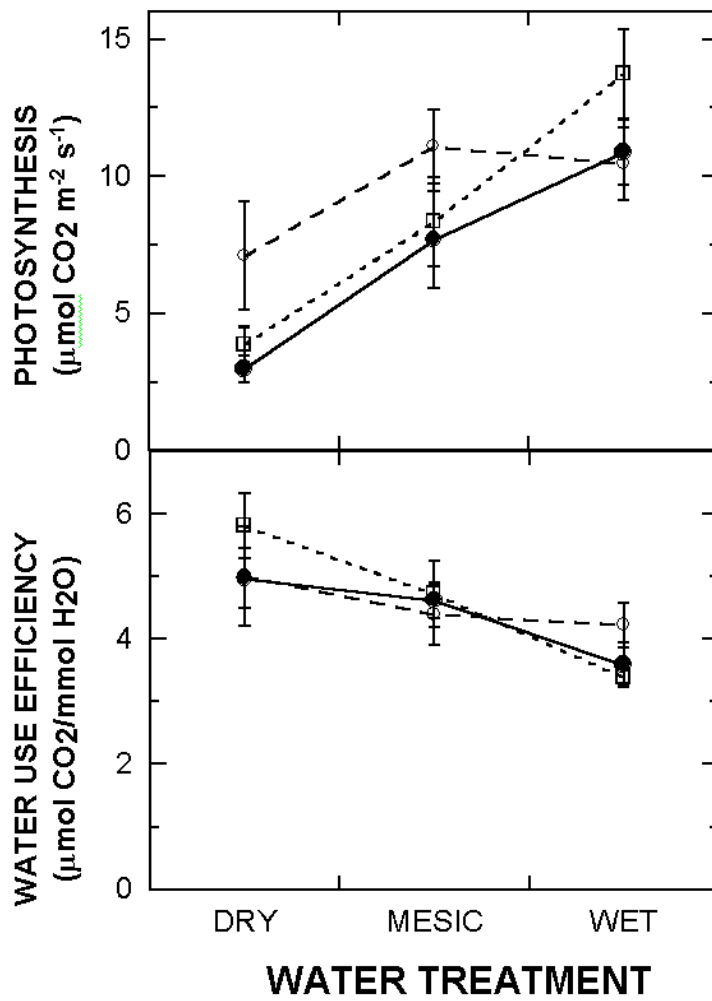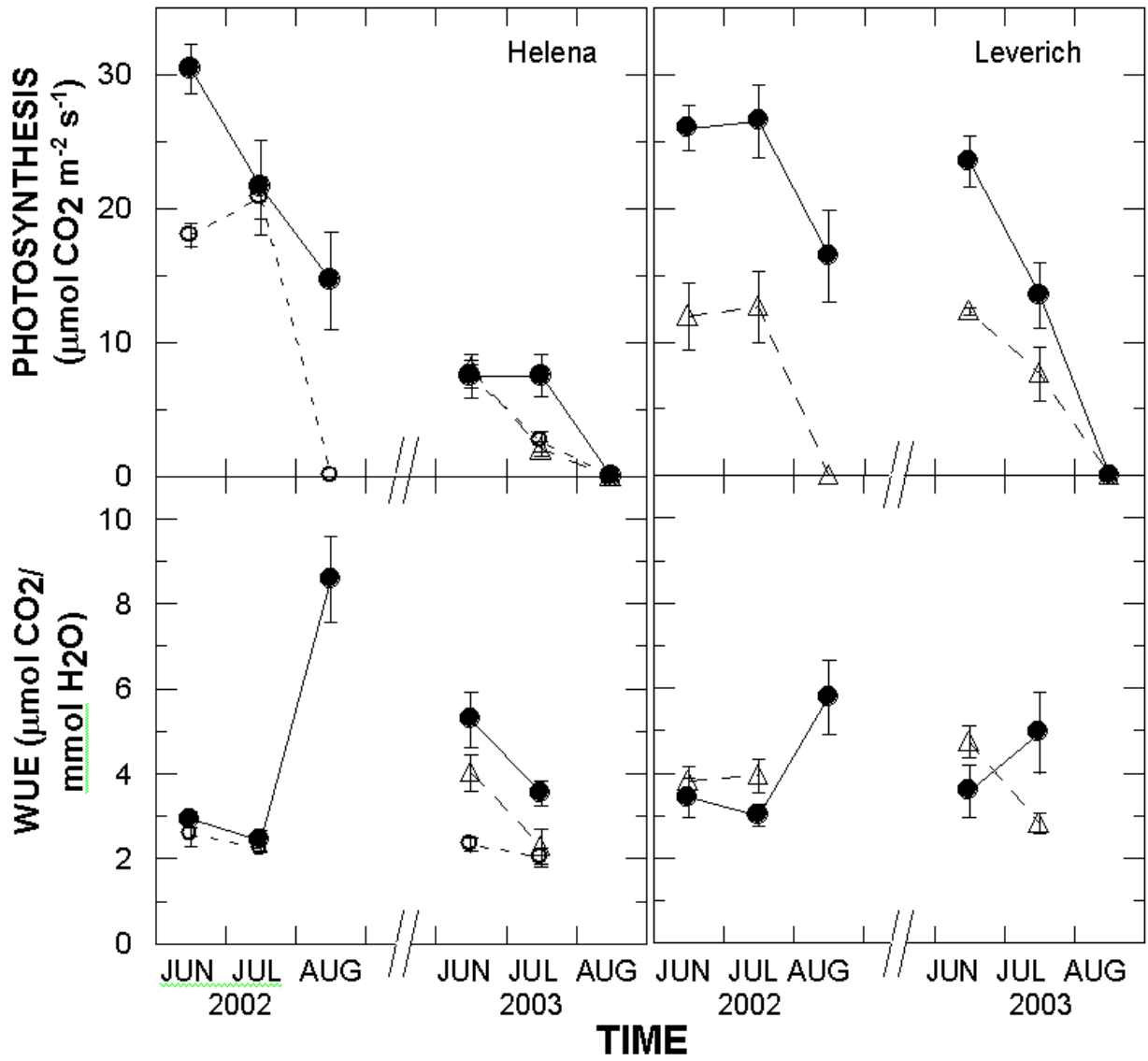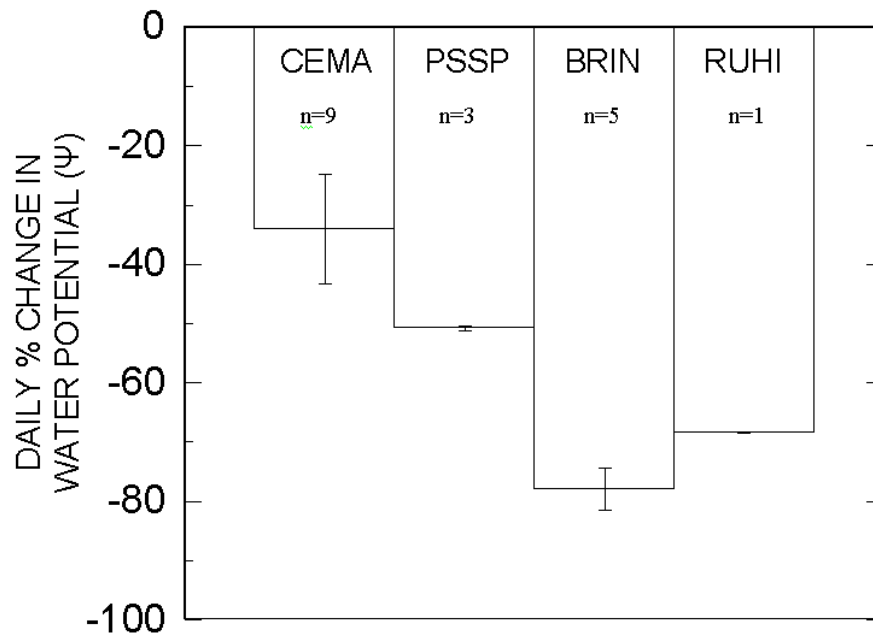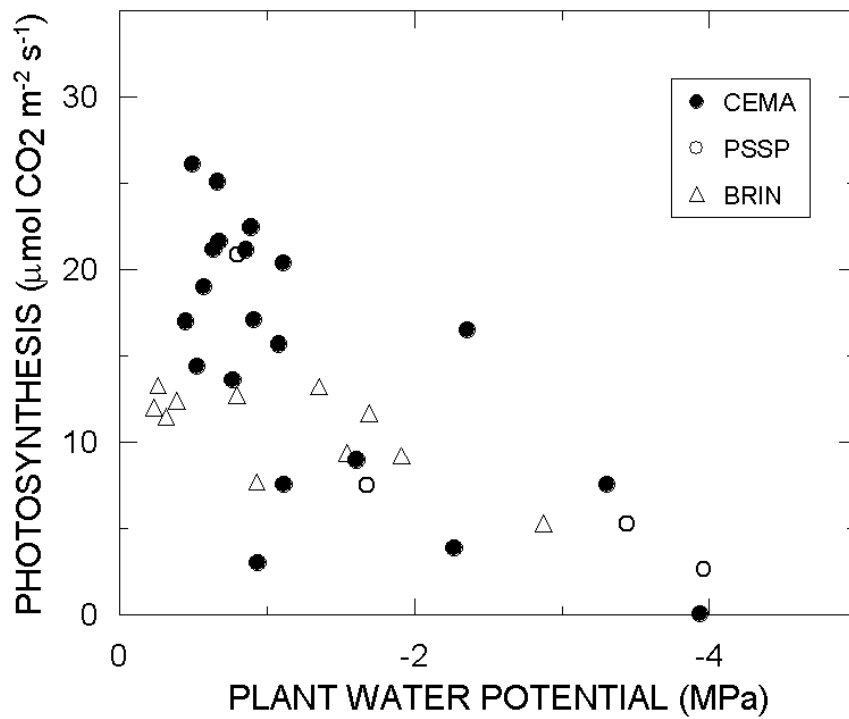
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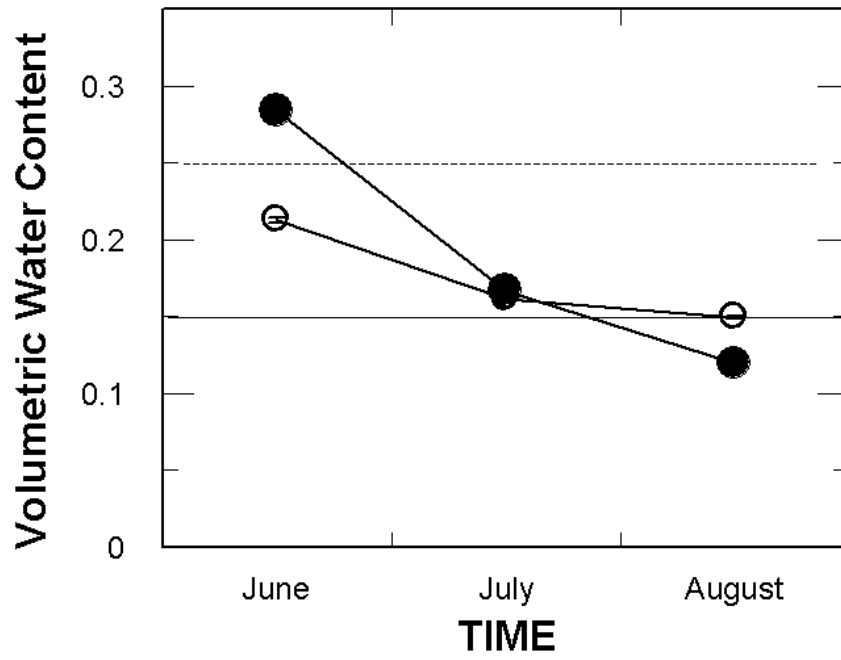
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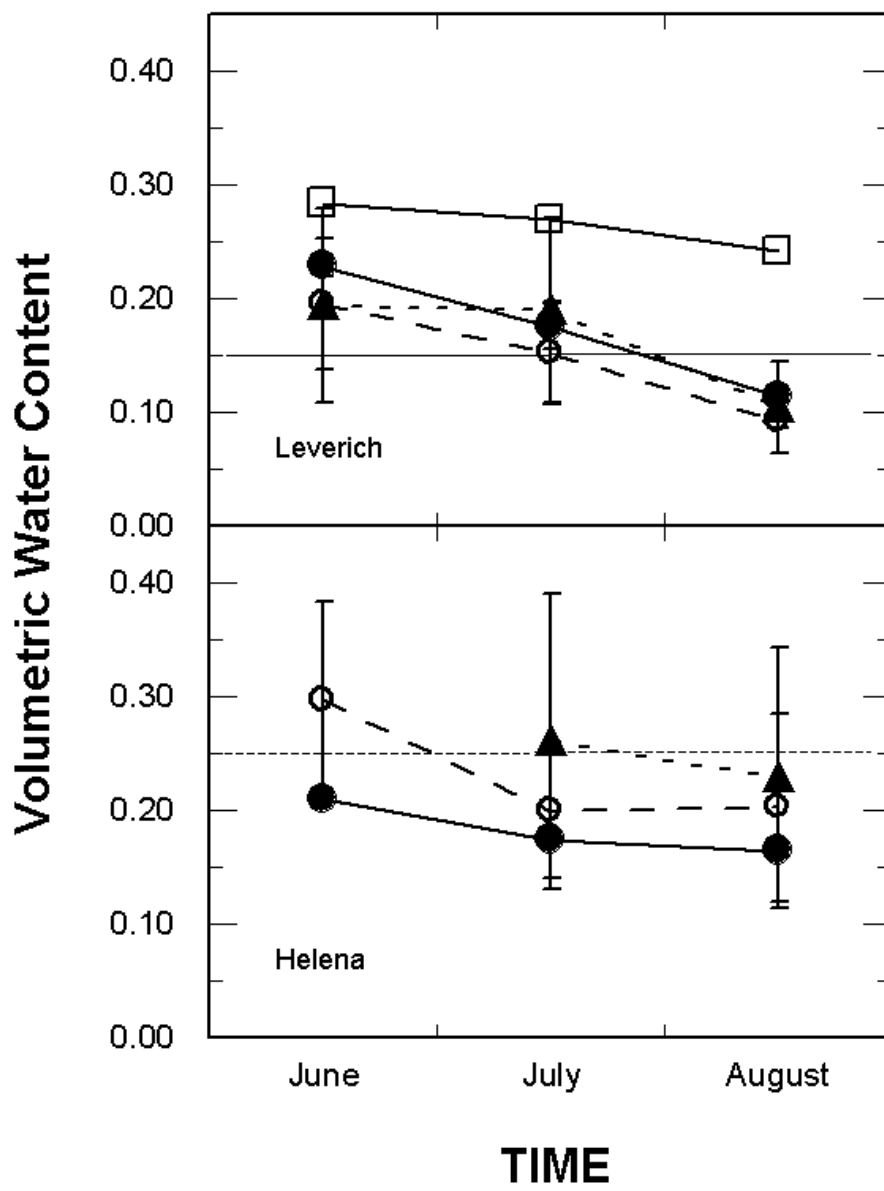
Figure 3

Figure 4

Figure 5

Figure 6